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VOL. 22, SEC. C. FEBRUARY, 1944 NUMBER 1

SUGAR PRODUCTION BY WHITE AND YELLOW BIRCHES[1]

BY L. P. V. JOHNSON[2]

Abstract

White and yellow birch trees produced an abundance of sap, but the yield of sugar was on the average only about one-third that of the sugar maple. Results indicate that yellow birch sap contains invert sugar with small amounts of sucrose, and that white birch sap contains a mixture of fructose and invert sugar. Syrups prepared from white and yellow birch saps by concentrating 100 times were similar in taste and appearance to commercial corn syrup.

Introduction

In 1941 during the course of experiments on sap flow and sugar production in the sugar maple, a number of white and yellow birches were included, since very little was known about the flow and composition of birch sap. At the time, the data obtained from the birches were considered to be of little interest or practical importance. However, with the present shortage of sugar, it appears that there is a growing interest in the matter. The results are, therefore, now reported for whatever value they may have.

Materials and Methods

Twelve white birches, *Betula papyrifera* Marsh., two yellow birches, *B. lutea* Michx., and four sugar maples, *Acer saccharum* Marsh., growing on roughly the same site were used in these studies. Ages of the trees were determined from increment borer cores, and crown indices by a rough estimation of total leaf areas. Heights were measured by a hypsometer, and diameters at breast height (*D.B.H.*) by a diameter tape.

The trees were tapped according to the standard method for the sugar maple. Total sap production was measured cumulatively as the sap was collected. Determinations of pH were made electrometrically. The optical rotatory power of the saps was determined at 20° C. using 2-dm. tubes. Analyses for reducing sugars before and after acid hydrolysis were conducted by the method of Shaffer and Hartmann (6). Determinations of the over-all specific rotation of birch sugar were based on the total sugar determinations by the Shaffer–Hartmann method and the polarization values for the saps before and after acid hydrolysis.

[1] *Manuscript received October 26, 1943.*

Contribution from the Division of Applied Biology, National Research Council Laboratories, Ottawa. Part of a co-operative project of the Subcommittee on Forest Tree Breeding, Associate Committee on Forestry, N.R.C. No. 1179.

[2] *Forest Geneticist.*

Experimental Results

The general description of the trees, volume of sap produced, and pH of fresh sap are given in Table I. It will be noted in each species that the younger trees tend to produce as much or more sap than the older, larger trees. In white birch, trees of about 9 or 10 in. in diameter would appear to be a good size for tapping. The determinations of pH were made to ascertain whether acidity of the sap might be related to the higher content of invert sugar in birch as compared to the maple (see Table III). However, the pH varied little, with an extreme range of 6.8 to 7.6, which is approximately that found in maple sap.

TABLE I

GENERAL DESCRIPTION OF, AND QUANTITY AND pH OF, SAP PRODUCED BY INDIVIDUAL TREES OF WHITE BIRCH (*BW*), YELLOW BIRCH (*BY*), AND SUGAR MAPLE (*MS*) IN 1941

Material	Age	*D.B.H.*, in.	Ht., ft.	Crown index	Total sap, litres	pH, fresh sap
BW–26	37	11.6	55	95	42.8	7.57
–28	52	17.8	50	130	54.6	6.92
–29	33	10.0	67	85	109.0	6.97
–30	33	9.1	70	85	40.0	6.89
–31	33	9.1	68	85	60.8	6.86
–33	33	10.7	70	85	48.6	7.21
–34	35	9.3	70	85	58.1	6.84
–35	33	9.0	60	85	105.8	—
–36	33	8.9	60	80	52.1	6.92
–37	33	8.7	62	80	17.6	6.84
–38	33	8.1	62	90	70.0	—
–39	45	15.5	60	130	97.1	—
BY–27	55	18.7	47	130	40.9	7.21
–32	33	9.0	65	80	75.1	6.89
MS–47	72	15.8	65	120	8.6 (40.6)*	7.48
–48	59	13.9	60	110	11.4 (59.1)	7.37
–49	40	9.6	60	100	22.9 (48.6)	6.70
–50	40	9.4	60	95	17.9 (43.6)	6.67

* *The figures in parentheses are 1942 data, which approximate normal sap production more closely than the 1941 results.*

The 1941 sap flow season was considerably longer for birch (Mar. 29 to April 25) than for maple (Mar. 29 to April 15).

The volume of sap produced by the birch trees compared very favourably with that produced by maples, judging from the data in Table I, and from the information given by Bryan (1). This author states that from 10 to 20 gal. of sap may be expected on an average per maple tree. This corresponds to 38 to 76 litres, which pretty well covers the range of yields recorded here for the birches. The yield from certain of the birch specimens exceeded this average range for the maple but none have exceeded the sap production of unusually good maples as reported by Bryan.

The yield of sap in 1941 from the maple trees under study was abnormally low and, therefore, does not provide a sound basis for evaluating the relative sap production of the birches. The 1942 sap yields of these trees, considered to be normal, are, therefore, inserted in Table I for this purpose.

The kinds and amounts of sugars in maple products have already received thorough treatment. After examining 80 samples from different parts of Quebec, Bryan (2) gives the following average analyses for Canadian maple sugar: sucrose, 86.48%; invert sugar, 8.76%; ash, 1.06%; and undetermined matter, 3.70%. Polarimetric data on hydrolysed and natural saps, given in Table III, indicate that the sugar maples used in the present study had a very high proportion of sucrose.

The only information on birch saps that has been found in the literature is that given by Lenz (4) who concluded that the sugar in birch sap is principally, if not entirely, fructose. Other authors who mentioned sugars in the birch were concerned with various plant parts rather than with the sap. Gibbs (3) working on *Betula populifolia* found, among the alcohol-soluble sugars of the twigs, that sucrose was present in much greater amounts than reducing sugars, except in May and June when sucrose dropped below the level of the less fluctuating reducing sugars. Sosa and Sosa-Bourdouil (7) report the sugars of *B. alba* to consist mainly of reducing sugar together with some sucrose.

Measurements of the reducing power and optical activity before and after acid hydrolysis of freshly collected birch saps of the 1943 season are presented in Table II. In interpreting this table, it has been necessary to assume that other organic substances did not interfere significantly with the polarization and reducing sugar values. From these results, it is evident that reducing sugars were present almost exclusively in the white birch saps. In the single yellow birch tree studied, there is evidence of the presence of small amounts of sucrose, but here again, reducing sugars are preponderantly the chief

TABLE II

TOTAL AND REDUCING SUGARS OF 1943 BIRCH SAPS, AND CORRESPONDING POLARIZATION VALUES

Sample		Reducing sugars by copper reduction (%)	α 1 dm.	Apparent $(\alpha)20^*$ D
BW–29	Nat.	0.840	−0.36	−42.15°
	Hyd.	0.854	−0.335	−39.22°
BW–35	Nat.	1.005	−0.385	−38.21°
	Hyd.	1.008	−0.385	−38.21°
BY–1	Nat.	0.919	−0.18	−19.25°
	Hyd.	0.935	−0.215	−23.00°

* *Specific rotation calculated as* $\frac{100 \times \alpha}{\textit{Total sugar content}}$.

constituent. Evidence for the relative proportions of glucose and fructose is limited to the calculated specific rotation values. Since fructose has a specific rotation of $-92.9°$ approximately, while the corresponding values for sucrose and invert sugar are $+66.5°$ and $-20.1°$, respectively (5, p. 160), it would appear that fructose predominated in the mixture of reducing sugars present in the white birch saps. In the yellow birch sample, fructose and glucose were apparently present in equal quantities (i.e., invert sugar), along with small amounts of sucrose.

The additional data on birch saps (Table III), while more extensive, are less trustworthy since they rest entirely on polarization values. To obtain an estimation of the sugar content of these saps, the calculated specific rotation values for the white and yellow birches of Table II have been applied to the polarization values of Table III. These specific rotation values are based on saps collected in a subsequent year and at only one stage of the tapping season. The possibility of differing proportions of sugars between the individual trees, between years, and between periods within a single tapping season cannot be precluded.

During the 1941 tapping season, the sugar content of the various saps underwent considerable variation. In white birch, the mid-season collection showed constant increases in percentage sugar over the early collection. It is of interest to note that *BW*-35, a heavy sap yielder, is also one of the highest in percentage sugar. Of the two yellow birches, the sap of one increased while the other decreased in percentage sugar content as the season advanced.

In order to compare the sugar content of birch saps with that of the sugar maple, the sugar percentage of the maple saps given in Table III should be supplemented by reference to the work of Bryan (1). He states that normal maple sap of an average year contains about 2% sugar, although it may vary from 0.5 up to as high as 7 or even 10%. The 1943 data for birch saps, which are based on quantitative measurements, show the sugar content to be less than half that of "average" maple sap. The sugar content of the birch saps for 1941 shows considerable variation but on the whole it can be said to be only one-quarter to one-half that of average maple sap.

Palatable syrups were prepared in the laboratory by concentrating yellow and white birch saps down to the consistency of commercial maple syrup. Maple saps were found to require concentration of 30 times while for birch saps concentration of 100 times was necessary. The white birch syrup was very much like ordinary corn syrup in both colour and flavour. The yellow birch syrup was darker and had a suggestion of unpleasant flavour, but there was no trace of the wintergreen flavour that is present in the young bark. The colour and flavour of maple syrup is difficult to control in the evaporator and undoubtedly the same applies to the birch syrups, so that the differences noted between the white and yellow birch may not prove to be consistent characteristics of the two species.

TABLE III

POLARIMETRIC DATA* ON 1941 BIRCH AND MAPLE SAPS, WITH DERIVED DATA AS TO SUGAR CONTENT

Sample	Early				Mid-season				Late		Average % sugar all coll. (natural)
	Natural		Hydrolysed		Natural		Hydrolysed		Natural		
	α (1 dm.)	% Sugar*	α	% Sugar*	α	% Sugar*	α	% Sugar*	α	% Sugar*	
BW–26	−0.175	0.43	−0.17	0.44	−0.31	0.77	—	—	−0.315	0.78	0.66
–28	−0.31	0.77	−0.32	0.83	−0.445	1.11	—	—	—	—	0.94
–29	−0.24	0.60	−0.245	0.63	−0.265	0.66	—	—	−0.26	0.65	0.64
–30	−0.205	0.51	−0.215	0.56	−0.295	0.73	—	—	−0.32	0.79	0.68
–31	−0.19	0.47	−0.18	0.47	−0.23	0.57	—	—	−0.225	0.56	0.53
–33	−0.31	0.77	−0.31	0.80	−0.33	0.82	—	—	−0.275	0.69	0.76
–34	−0.28	0.70	−0.285	0.74	−0.28	0.70	—	—	−0.30	0.75	0.72
–35	−0.28	0.70	—	—	−0.33	0.82	—	—	−0.325	0.81	0.78
–36	−0.21	0.52	−0.21	0.54	−0.28	0.70	—	—	−0.33	0.82	0.68
–37	−0.24	0.60	−0.24	0.62	−0.225	0.56	—	—	—	—	0.58
–38	−0.225	0.56	—	—	−0.215	0.53	—	—	—	—	0.55
–39	−0.225	0.63	—	—	−0.215	0.53	—	—	—	—	0.58
Average	—	0.61	—	0.63	—	0.71	—	—	—	0.73	0.68
BY–27	−0.325	1.62	−0.325	1.62	−0.13	0.65	—	—	−0.12	0.60	0.96
–32	−0.18	0.90	−0.18	0.90	−0.29	1.44	—	—	−0.285	1.42	1.25
Average	—	1.26	—	1.26	—	1.05	—	—	—	1.01	1.11
MS–47	+6.69	5.03	—	—	+5.89	4.43	−1.86	4.63	+4.82	3.62	4.36
–48	+3.04	2.29	—	—	+3.40	2.56	−1.05	2.61	+3.58	2.69	2.51
–49	+2.21	1.66	—	—	+3.24	2.44	−1.02	2.54	+3.05	2.29	2.13
–50	+3.26	2.45	—	—	+3.16	2.38	−0.96	2.39	+2.90	2.18	2.34
Average	—	2.73	—	—	—	2.95	—	—	—	2.70	2.79

* *Calculated from the following specific rotations:*
White birch, natural −40.2; hydrolysed −38.7 (average of values given in Table II).
Yellow birch, natural and hydrolysed, −20.1 (invert sugar).
Sugar maple, natural, +66.5 (sucrose); hydrolysed, −20.1 (invert sugar).

Discussion

From the foregoing, it appears that birch sap, while consistently lower than maple sap in sugar content, is produced in quantities that, on a long range average, should be of the same order per tree as the sap yield of the sugar maple. According to Bryan (1), a grove of 100 maple trees should produce about 40 gal. of syrup or 300 lb. of sugar. From the present work, it appears that less than half of this amount of syrup or sugar could be expected from a similar stand of either the white or yellow birch.

The birches are more widely distributed in Canada than the sugar maple, and there is no doubt that large quantities of palatable syrup could be prepared from them, but the amount of fuel and labour required would ordinarily be prohibitive. Under the conditions of the present sugar shortage, however,

the production of birch syrup might be undertaken to advantage in certain localities where especially favourable circumstances exist.

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MELANISM IN WHEAT INDUCED BY HIGH TEMPERATURE AND HUMIDITY[1]

By T. Johnson and W. A. F. Hagborg[2]

Abstract

Results of experiments performed in the greenhouse have shown that, under conditions of a high temperature especially when combined with a high humidity, melanistic areas may develop on the glumes, lemmas, peduncles, and internodes of Apex and Renown wheat in the absence of any infection by pathogenic organisms.

Introduction

It has been demonstrated (4, 5, 6) that the melanism characteristic of some newly developed wheats—particularly those derived from crosses of common wheats with Hope and *H*-44—may be caused by infection with *Puccinia graminis Tritici* Erikss. and Henn. and *Alternaria tenuis* Nees. The writers, however, have never been convinced that all the melanistic reactions shown by such varieties were so produced. In areas where no stem rust was present, there have, occasionally, appeared on glumes, rachides, and internodes, dark discolorations from which pathogenic bacteria and fungi could not be isolated. Moreover, experimental evidence indicating that environmental factors, particularly light and temperature, could influence the production of melanism, has gradually accumulated.

Broadfoot and Robertson (1) have expressed the opinion that environmental factors, principally light intensity, induce the production of a form of melanism to which they have given the name "pseudo-black chaff".

Hagborg (2) produced experimental evidence that purely environmental factors could induce the type of melanism characteristic of Hope, *H*-44, and their derivatives. He stated that "internodal melanism" developed on internodes, peduncles, and rachides of Pentad × Marquis (*R. L.* 723) after plants had been kept in moist chambers for periods varying from 36 to 60 hr. at a temperature of 25° C. No melanism, however, developed on the glumes and lemmas. From these results he inferred that the discoloration was induced by the conditions of high temperature and humidity to which the plants were subjected in the moist chambers.

Recently, Hart and Allison (3), in discussing the effect of wheat stem rust infection on the production of brown discoloration on seedling leaves of wheat, stated that high temperature (above 28.5° C.) was the one factor of the environment responsible for the discoloration surrounding the infection centres. The degree of pigmentation varied directly with the length of time the temperature remained above 28.5° C. Moderately high atmospheric humidity was found

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to accelerate the expression of the "browning reaction", but did not induce the reaction in the absence of the primary stimulus of high temperature.

Melanism Caused by High Temperature and Humidity

In an attempt to secure information on the influence of temperature and humidity on the production of melanism in wheat heads, an experiment was carried out with the rust resistant varieties Apex and Renown, which frequently show melanism, and the susceptible variety Marquis, which does not. The plants were grown in 6-in. pots, four plants per pot, in the greenhouse at moderate temperatures and a moderately high humidity. At the time of heading, half of the plants of each variety were removed to a greenhouse maintained at a considerably higher temperature, the other half were left where they were.

To obtain two different conditions of humidity in each greenhouse, half of the heads in each were covered with glassine bags and half were left uncovered. Each bag was tied, below the head and around a cotton wad that encircled the peduncle. To ensure a higher humidity around the bagged heads, the cotton wads were frequently moistened by injection of water with a hypodermic needle. For the heads, conditions were therefore obtained of (*a*) high temperature + high humidity, (*b*) high temperature + moderate humidity, (*c*) moderate temperature + high humidity, (*d*) moderate temperature + moderately high humidity. The glassine bags had the effect not only of raising the humidity but also of raising the temperature, at least during periods of sunshine. The temperature inside the bag was compared with that outside, in both shade and sunlight. In shade, the temperature within the bag was found to be 1° C., higher than outside, whereas, in the sunlight, it was 6.8° C. higher. The conditions of temperature and humidity within the bag apply only to the head and the uppermost part of the peduncle, which was also covered by the bag.

The experiment was begun on April 14. On May 3, all plants were cut down and examined for the presence of melanistic areas on glumes, lemmas, peduncles, and internodes. At that time the heads that appeared first had been out for 19 days, those that appeared last, for 14 days. The data relative to the presence of melanism on the various plant parts are given in Table I.

As shown in Table I, the discoloration of glumes, lemmas, peduncles, and internodes of both Apex and Renown was much more pronounced in the high temperature greenhouse than in the one kept at a moderate temperature, whereas no discoloration developed on Marquis plants in either greenhouse. From a comparison of the figures for glumes and lemmas of bagged and non-bagged heads, it is clear that the environment of the bagged heads was particularly conducive to the production of melanism. This environment differed in at least two respects from that of the non-bagged heads in the same greenhouse. (1) The bagging, as already pointed out, had the effect of raising the temperature especially during periods of sunlight, so that the

TABLE I

THE EFFECT OF TEMPERATURE AND HUMIDITY ON THE DEVELOPMENT OF MELANISM IN APEX, RENOWN, AND MARQUIS WHEATS (NUMBER AND PERCENTAGE OF PLANT PARTS DISCOLOURED)

Variety	High temperature Mean daily max., 34.4° C. Mean daily min., 19.0° C. Mean temperature, 26.7° C. Mean relative humidity, 60%				Moderate temperature Mean daily max., 30.3° C. Mean daily min., 9.8° C. Mean temperature, 20.1° C. Mean relative humidity, 85%			
	Heads bagged*		Heads not bagged		Heads bagged*		Heads not bagged	
	No. discol.	% discol.	No. discol.	% discol.	No. discol.	% discol.	No. discol.	% discol.
Apex	10 heads		7 heads		10 heads		9 heads	
Glumes	59	17.4	1	0.4	16	4.9	1	0.3
Lemmas	21	6.7	5	2.2	8	2.6	0	0.0
Peduncles	2	20.0	0	0.0	0	0.0	0	0.0
1st internode	9	90.0	6	85.7	0	0.0	2	22.2
2nd internode	8	80.0	7	100.0	0	0.0	0	0.0
Renown	9 heads		6 heads		9 heads		9 heads	
Glumes	170	50.3	7	3.1	13	4.0	0	0.0
Lemmas	39	11.7	4	1.8	2	0.6	0	0.0
Peduncles	4	44.4	1	16.7	0	0.0	0	0.0
1st internode	2	22.2	0	0.0	0	0.0	0	0.0
2nd internode	0	0.0	0	0.0	0	0.0	0	0.0
Marquis	10 heads		7 heads		9 heads		7 heads	
Glumes	0	0.0	0	0.0	0	0.0	0	0.0
Lemmas	0	0.0	0	0.0	0	0.0	0	0.0
Peduncles	0	0.0	0	0.0	0	0.0	0	0.0
1st internode	0	0.0	0	0.0	0	0.0	0	0.0
2nd internode	0	0.0	0	0.0	0	0.0	0	0.0

** The temperature and humidity for the bagged heads were both somewhat above the figures given in the table, which represent the conditions prevailing in the greenhouses and apply to the non-bagged heads and all internodes.*

temperatures for the bagged heads would be somewhat in excess of the figures given in Table I; and (2) the presence of a moist cotton wad provided the bagged heads with an atmosphere high in humidity. No measurement was made of the relative humidity of the air within the bags, but it was without doubt considerably above the figures given in Table I. This combination of a high temperature with a high atmospheric humidity was capable of producing on both Apex and Renown a head discoloration very similar to that frequently encountered on specimens collected in the field. Pronounced melanism developed also on internodes, particularly on Apex, in the high temperature greenhouse. That the melanism was induced by the environment and not by any accidental infections of pathogenic organisms was con-

firmed by isolation studies in which neither fungi nor bacteria were obtained from any of the plant parts plated. The plating studies do not, of course, entirely exclude the possibility that the discoloration might have been caused by infection with stray rust spores. This possibility, however, is remote, as bagged heads of the susceptible variety Marquis developed no rust pustules and, in any case, the bagging of the heads as they emerged would have the effect of preventing the lodgment of spores on them. The conclusion, therefore, seems justified that the discoloration developed in the absence of rust infection and as a result of the high temperature and humidity.

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THE PRAIRIE AND ASSOCIATED VEGETATION OF SOUTHWESTERN ALBERTA[1]

By E. H. Moss[2]

Abstract

This is a contribution to an understanding of the floristic composition and ecology of the chief plant communities in the region. Three major grassland types are recognized and correlated with climatic factors, topography, and soil colour zones,— the *Bouteloua–Stipa* association in the dark brown soil zone, the *Festuca–Danthonia* association in the black soil zone, and the *Agropyron–Stipa–Carex* associes in the intermediate shallow black soil zone. Of some 250 species and varieties of vascular plants found in these grassland communities, approximately 125 are regarded as either common or characteristic. Poplar and coniferous vegetation is considered in relation to climate, physical features, and the associated grassland. The limber pine and Douglas fir communities of rocky ridges in the "parkland" are described. Prairie and poplar associations are compared with corresponding vegetational types described for other regions. Brief consideration is given to probable migration routes of certain species, and to current fluctuations and trends in the flora of the region.

Introduction

A botanical survey, sponsored by Science Service, Ottawa, was initiated in the late summer of 1939 and continued in June of 1940 and the early spring of 1941. The present paper deals with some of the salient features of the natural vegetation in the area covered by the survey. The region involved is mainly that extending northward from Waterton Lakes Park to the Oldman River, comprising certain western portions of the Lethbridge sheet and adjoining parts of the Pincher sheet (Fig. 1). The most critical work was done in the vicinity of Pincher Creek, north to the Oldman River, east to Macleod, Standoff, and Hillspring, and south towards the Park. Less intensive work was carried out north of the Oldman River at the southern extremity of the Porcupine Hills, in Waterton Lakes Park and vicinity, and near Cardston east of the Park.

This account of the vegetation of the region may properly be regarded as preliminary in nature. An adequate description and interpretation of the flora in its various aspects would require much more extensive and detailed work. In certain respects, this paper may serve to supplement the recently published reports of Clarke and his associates (3, 4). It also relates closely to the earlier work of the present writer (9) on the poplar and prairie vegetation of central Alberta. A wise land-use policy can be formulated only in the light of extensive knowledge of the soils, flora, fauna, and other natural resources. The present contribution aims to supply information on the natural vegetation of a region whose soils and certain other features have already been well investigated but whose biological resources have not been critically examined or interpreted.

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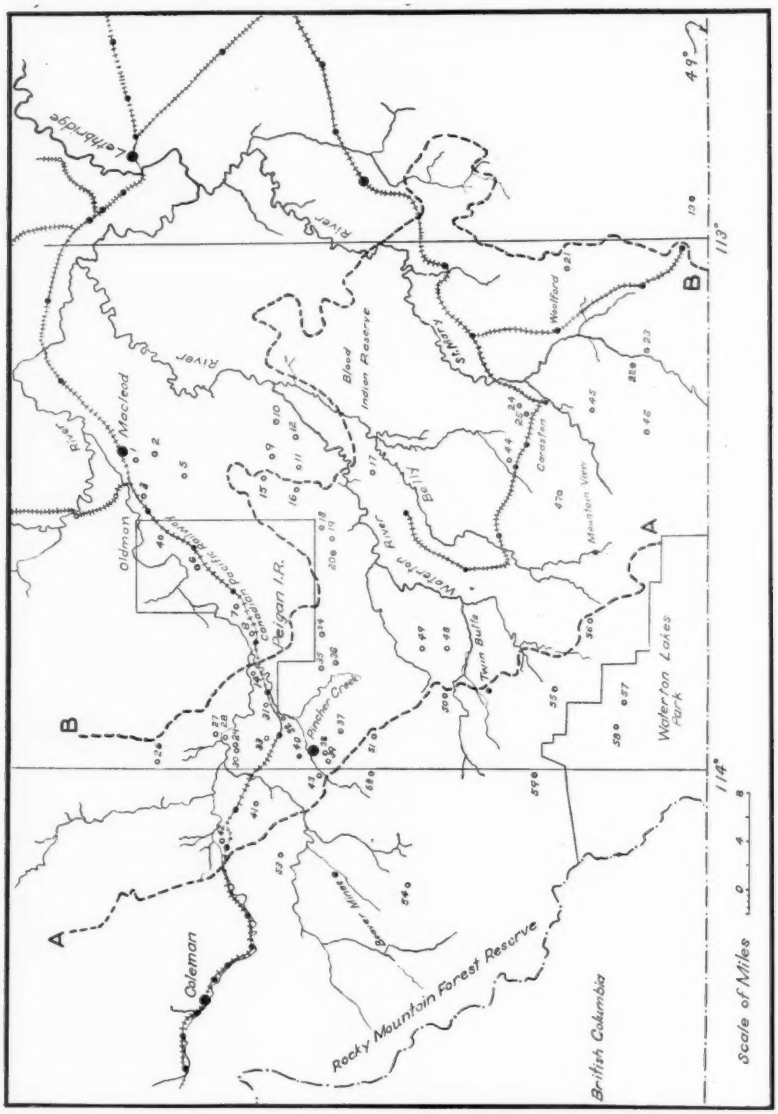

FIG. 1. *Map of southwestern Alberta. Grassland areas critically examined are shown as numbered circles. Boundary between the deep black and shallow black soil zones is shown by the line (A), and the boundary between shallow black and dark brown soil zones by the line (B).*

Topography and Soils

The investigation extended over about 1500 square miles of high undulating plain and foothills adjoining the mountains in southwestern Alberta (Figs. 1, 2, 3, 8, and 9). The transition from plain to mountains is abrupt, especially near Waterton Lakes Park. Northward, from the Park to Beaver Mines and Burmis, there is a narrow range of foothills, in the form of rocky ridges, paralleling the mountains. Touching the area on the north is the southern spur of the Porcupine Hills, and on the southeast the western tip of the Milk River ridge. There is a general slope of the area from east to west and southwest, the altitude ranging from about 3100 ft. at Macleod to about 4200 ft. at Beaver Mines and at the edge of Waterton Lakes Park, with the adjacent mountains rising abruptly to altitudes of about 8000 ft.

The area is drained by the Oldman River, tributary to the Saskatchewan River system. Traversing the area and flowing westward and northwestward into the Oldman River are the Crowsnest, Castle, Waterton, Belly, and St. Mary Rivers. Numerous mountain and foothill streams, fluctuating in size and running in deep valleys, flow into the rivers. These stream valleys and the numerous rocky ridges give to most of the area near the mountains a rough topography. Eastward the area is rolling to flat, apart from the river valleys.

Much of the region is covered with glacial deposits of Pleistocene age. Both Cordilleran and Continental (Keewatin) glaciers are said to have advanced over the area, leaving morainal, till, and boulder clay deposits. Rutherford (11) considers that the Cordilleran glaciation antedated the main advance of the Keewatin ice-sheet, and that the latter extended in the Waterton district to the front range of the Rocky Mountains. According to Allan (17), large areas of the region are covered by resorted glacial deposits, other large areas by alluvial and lacustrine deposits transported by running water, while smaller areas are occupied by residual material developed from the underlying rock formations. Allan states that it is not always possible to determine the origin of the surface deposits because frequently the unconsolidated material is of mixed origin.

From these various deposits, through the action of climatic and biotic factors, the soils of the region have developed. Wyatt, Bowser, and Odynsky (17) recognize four soil colour zones, namely, brown, dark brown, shallow black, and black, of which the last three zones are represented in the region covered by this paper (Fig. 1). The colour differences are correlated with the soil moisture conditions and the vegetational types that have prevailed through a long period of time. The black soils differ from the brown soils in their colour, deeper profile, and greater accumulation of organic matter, and in having developed under more humid conditions. The soils of the colour zones are further classified by Wyatt *et al.* according to (*a*) the texture of the surface soil, (*b*) the dominant characteristics of the soil profile, (*c*) the mode

of deposition of the parent material. This soils classification has been extremely useful in the present investigation and will be referred to, in greater detail, later in the paper.

Climate of Region

Available data on the climate of the region have been brought together and adequately discussed by Wyatt *et al.* (17). In general, the climate may be described as rigorous, owing to wide and rapid fluctuations in temperature, marked annual and seasonal variations in precipitation, prolonged periods of drought, and strong, drying winds. Only those climatic features of special importance in connection with the natural vegetation will be elaborated here.

The climate is characterized by warm summers with cool nights and cold winters marked periodically by the ameliorating effects of warm winds, the "Chinooks". Wide, and sometimes rapid, fluctuations in temperature occur from time to time throughout the year. The mean annual temperature increases slightly from west to east in the region. Available records show a mean winter temperature of about 24° F., and a mean growing season temperature of 54.6° at Macleod and 50.2° at Pincher Creek. The length of the frostless season varies greatly from year to year and also varies locally with changes in relief or topography.

The average annual precipitation increases from the region of Lethbridge westward and southwestward to the Rocky Mountains, as shown by the following records: Lethbridge and Macleod, about 15.5 in.; Cardston, 18.5; Pincher Creek, 20; Beaver Mines, 21; Waterton, 30 in. There are wide differences from year to year in the total annual precipitation. For example, at Pincher Creek, the precipitation ranged from 9.4 in. in 1904 to 34.3 in. in 1927. From one-third to one-half of the precipitation occurs in the form of snow, and the snowfall increases, both in amount and in proportion of the total precipitation, from east to west in the region. The seasonal distribution of the precipitation is of considerable interest. In the Lethbridge–Macleod–Pincher Creek area, over 75% of the total precipitation falls in the growing season, April to July inclusive, and during the previous autumn; this portion of the precipitation is considered to be highly effective in connection with plant growth. Closer to the mountains, as at Beaver Mines, the corresponding portion of the total precipitation is only 62%, but there is a much heavier snowfall, with compensating effects. Moreover, in and near the foothills, the greater part of the precipitation for the growing season comes in the spring, while midsummer is dry.

Factors of great importance are wind velocity and evaporation rate. The prevailing winds are westerly, of high velocity, warm, and extremely dry. During the winter, these winds produce rapid elevations in temperature and quick melting of snow. Indirectly they may produce winter killing of plants through a breaking of dormancy prior to the normal growing season. In the spring, they may increase the availability of moisture by rendering the

soil more receptive to rain and melting snow. During summer, these winds have a very marked desiccating effect on the soil and vegetation.

Survey Methods

Since attention was primarily directed to the native flora of the region, an effort was made to locate samples of the chief vegetational types that appeared to have suffered little or no disturbance. Actually only a small percentage of the vegetation remains in the virgin state. In parts of the region, cultivation has led to the restriction of the native vegetation to roadsides, railroad right-of-ways, and small areas of inaccessible or rough land. Elsewhere the virgin flora has been altered in varying degrees by drainage, mowing, burning and grazing, especially the latter. Some investigation of disturbed areas was inevitable in the very act of trying to identify virgin vegetation; moreover, such study was of value in interpreting ecological phenomena. Correlations between the vegetation and other factors, as well as successional relationships, were kept in mind as important objectives of the field work.

Special study was given to sample areas of prairie that seemed to have suffered little disturbance in recent years and that approximated closely the natural state. Such areas were often encountered on wide road allowances and in corners of cultivated fields, often segregated by a coulee or a stream. These areas varied in size from a few hundred square feet to many acres. For each such area, the plant species were listed, their relative coverage and frequency (dispersion) estimated, and environmental conditions noted where these could be determined. Particular attention was given to topography, soil colour and texture, and to evidence of grazing, especially overgrazing. By means of belt transects across certain areas differing in slope and in soil texture, variations in the vegetation with topography and soil types were recorded. An effort was made to locate, and to study in some detail, samples of prairie on the chief soil types within the large soil zones (black, shallow black, dark brown) of the region. On the accompanying map (Fig. 1), 59 of these areas are shown, 10 in the black soil zone, 36 in the shallow black zone, and 13 in the dark brown zone. Other areas, less critically investigated, are not indicated on the map. The results of these studies, their analysis and interpretation, are presented in connection with the descriptions of the types of vegetation.

Prairie Vegetation

The following account of grassland vegetation is based, in the main, upon an analysis of data from the 59 stations shown on the accompanying map (Fig. 1). The general procedure employed in the selection and investigation of these sample areas has been explained above. For each sample area, the "frequencies" of the species were recorded by the following symbols.

Symbol	Meaning	Percentage coverage
d	Dominant	50
cd	Co-dominant	30
va	Very abundant	20
a	Abundant	10
f	Frequent, quite common	5
s	Scattered, fairly common	1
o	Occasional, uncommon	0.1
r	Rare and very rare	0.01

Each of the symbols records an estimate of the abundance, density, and dispersion of a species, and is taken to represent approximately the percentage coverage indicated. For the leading species, "frequency" symbols were converted to the corresponding numerical coverage values, and graphs constructed. In Table I coverage values are given for the chief grasses and sedges in 12 of the 59 stands investigated. Similar data for all of the 59 stands are incorporated in the graphical representation of Fig. 7, which shows the relative abundance of the characteristic grasses across the soil colour zones.

TABLE I

APPROXIMATE PERCENTAGE COVERAGE OF THE CHIEF GRASSES AND THE SEDGES IN FOUR REPRESENTATIVE STANDS OF EACH OF THE THREE GRASSLAND TYPES

Grassland type	*Bouteloua–Stipa* association				*Agropyron–Stipa–Carex* associes				*Festuca–Danthonia* association			
Soil zone	Dark brown				Shallow black				Black			
Stand numbers (Fig. 1)	4	6	8	11	19	21	25	35	50	51	58	59
Bouteloua gracilis	30	20	20	30	1	5	10					
Stipa comata	10	20	10	20		5	1	1				
Stipa viridula	0.1	5	5	0.1	1	5	5	1				
Agropyron Smithii												
dasystachyum Griffithsii	20	10	10	10	50	20	20	30	5	10	1	20
Koeleria gracilis	5	10	20	10	10	10	5	10	5	5	5	5
Stipa spartea v. *curtiseta*	1	0.1	1	5	5	10	5	5	0.1	1		
Poa spp.	1	5	5	0.1	5	5	10	5	5	5	1	5
Agropyron trachycaulum			1		0.1	1			0.1	5	5	1
Avena Hookeri			0.1				0.1		1	5	1	1
Festuca idahoensis				1	5	5	20	5	20	10	5	20
Festuca scabrella					0.1	1	0.1	0.1	20	10	50	10
Danthonia spp.						1	0.1		20	20	10	20
Stipa columbiana									1	5	1	1
Carex Eleocharis and *Carex* spp.	5	1	5	1	5	5	5	10	5	5	1	1
Percentage grass and sedge cover	72	71	77	77	82	73	81	67	82	81	80	84

The method thus employed of assigning "frequency" symbols and coverage values subjectively is admittedly open to criticism. So also are the various statistical methods commonly used in the definition and diagnosis of plant communities. According to Ashby (1) and Clapham (2) there is no valid method at present available for using statistics in the classification of vegetation, although quantitative methods may be used in studying the distribution of individual species. Ashby expressly states that the classification of plant communities depends on subjective criteria. In the present investigation, necessarily preliminary and brief in character, only subjective methods were feasible.

The marked change in grassland composition across the soil colour zones (Fig. 7) is of particular interest. While certain of the grasses, notably *Koeleria gracilis*, flourish across the entire region, most of the species are decidedly restricted in their zonal occurrence. The correlation of certain species with a soil colour zone would be still more strikingly shown, if account were taken of "islands" of adjoining soil types occurring one within the other. These relationships undoubtedly exist because both vegetation and soil profile characters of the region reflect in general the particular precipitation–evaporation conditions that have prevailed there through past centuries.

There are striking correlations between the vegetation and the soil texture, being especially marked in sandy loam and other light soils. Where these soils occur in the black and shallow black zones, the grassland is characterized by large proportions of *Stipa* spp. and sometimes by *Bouteloua gracilis*. There is also a close relationship between prairie vegetation and topography. In general, the steeper, south-facing slopes in the black soil zones have a large representation of *Bouteloua gracilis*, *Stipa comata*, and other species of *Stipa*, while the steeper, north-facing slopes in the dark-brown soil zone have a considerable coverage of fescue grasses. Even the small variations of micro-relief were often found to be accompanied by pronounced differences in grass flora.

Certain soils between Pincher Creek and Macleod have a high lime content (17) but there seems to be nothing distinctive about the natural vegetation of these soils. Further field work should be done on this and other similar problems.

The *Agropyron* group in the vegetation presents a number of intriguing problems. *Agropyron trachycaulum* is of secondary importance in the region, and much less abundant than in the prairie of central Alberta (9). *Agropyron spicatum* occurring sporadically in the western part of the region, is evidently an introduction from the Palouse prairie of the southwest. This species was occasionally found with distinct rhizomes, thus departing from the bunch habit, a characteristic of the plant reported from time to time and recently emphasized as common in the Festucetum of southeastern Washington and adjacent Idaho (8). *Agropyron dasystachyum*, *A. Griffithsii*, and *A. albicans* constitute a complex of intergrading forms. The first two of these species

are abundant in the region, including the western part, where they are often associated with the fescues. *Agropyron Smithii* and the variety *molle* are very prominent, especially in the shallow black and dark brown soil zones, where they dominate large areas. As shown in Fig. 7, *A. dasystachyum*, *A. Griffithsii*, and *A. Smithii* together make up a large portion of the grassland throughout the region and dominate in the shallow black soil zone. However, the writer believes that the very wide band representing the prevalence of these three *Agropyron* species somewhat exaggerates their importance. Certainly in the native prairie, and probably also in the present grasslands of the region, these grasses are to be assigned a less important place. The writer realizes now that a disproportionate number of the sample areas analysed were clay soils on which *Agropyron Smithii* rather than species of *Stipa* or *Festuca* are favoured, and also that many of the areas had been degraded by overgrazing and other factors, with an increase in the prevalence of *Agropyron*. As is explained more fully below, these species, and especially *A. Smithii*, are regarded as important elements in a disclimax that has its maximum development in the shallow black soil zone of the region.

Approximately 250 species and varieties of vascular plants were collected in the grassland vegetation. Of these, six species are weeds or introduced grasses, and about a dozen others are to be regarded as members of contiguous associations that have invaded the grassland locally. Still other species are very rare in the prairie of the region. Most of the common and characteristic species, about 125 in all, are mentioned in the following account of the associations.

The following prairie types are recognized: *Bouteloua–Stipa* association, *Festuca–Danthonia* association, and *Agropyron–Stipa–Carex* associes. This classification of grassland communities is to be regarded as tentative, and as a means of setting forth hypotheses regarding the natural grouping and successional changes. Additional grassland communities occur in small and localized areas.

Bouteloua–Stipa Association

This is considered to be the virgin and climax type of grassland for the dark brown soil zone. Actually, at the present time, the region provides rather few samples of this association in its natural form. The association (Fig. 4) is characterized by two dominant grasses, *Bouteloua gracilis* (H.B.K.) Lag. and *Stipa comata* Trin. & Rup. and two commonly associated grasses, *Koeleria gracilis* Pers. and *Agropyron Smithii* Rydb. (Table I). Accompanying grasses of lesser importance are *Stipa viridula* Trin., *Stipa spartea* Trin. var. *curtiseta* Hitchc., *Agropyron dasystachyum* (Hook.) Scribn., *A. albicans* Scribn. & Smith, *Calamagrostis montanensis* Scribn., *Muhlenbergia cuspidata* (Torr.) Rydb., and *Poa secunda* Presl. The leading sedge is *Carex Eleocharis* Bailey. *Carex filifolia* Nutt. is found locally. The only shrub of importance is the prairie rose, *Rosa arkansana* Porter, with *Symphoricarpos occidentalis* Hook., and *Elaeagnus argentea* Pursh occurring locally. Associated

species include the following, arranged in approximate order of their frequency, —*Gutierrezia diversifolia* Greene, *Erigeron caespitosus* Nutt., *Sideranthus spinulosus* (Pursh) Sweet, *Liatris punctata* Hook., *Solidago* spp., *Artemisia frigida* Willd., *A. gnaphalodes* Nutt., *Phlox Hoodii* Richards., *Malvastrum coccineum* (Nutt.) A. Gray, *Gaura coccinea* Nutt., *Comandra pallida* A. DC., *Achillea millefolium* L., *Potentilla* spp., *Drymocallis agromonioides* (Pursh) Rydb., *Lygodesmia juncea* (Pursh) D. Don, *Aster adsurgens* Greene, *Allium cernuum* Roth, *Selaginella densa* Rydb., *Chrysopsis villosa* (Pursh) Nutt., *Thermopsis rhombifolia* (Nutt.) Richards., *Linum* spp., *Petalostemon* spp., *Hedysarum boreale* Nutt. var. *cinerascens* (Rydb.) Rollins, *Astragalus pectinatus* Dougl., *Glycyrrhiza lepidota* Nutt., *Ratibida columnifera* (Nutt.) Woot. & Standl., and *Oenothera serrulata* Nutt.

This association forms part of the great community described by Weaver and Clements (16) and Clements and Shelford (7) as the "mixed prairie". These authorities would classify our *Bouteloua–Stipa* association as merely a subdivision or faciation of the "mixed prairie" which they consider to be an association.

Festuca–Danthonia Association

This is regarded as the natural and climax prairie for most parts of the black soil zones. Under prevailing conditions it is found in large areas of the deeper black soils (Figs. 2 and 3). The dominant grasses are *Festuca scabrella* Torr., *F. idahoensis* Elmer, *Danthonia intermedia* Vasey, and *D. Parryi* Scribn., of which the *Danthonia* species are localized in their dominance (Table I). Moreover, *Danthonia Parryi* appears to be largely restricted to the western part of the region, but might conceivably extend throughout the association in the course of time. Characteristic associated grasses are *Koeleria gracilis* Pers., *Agropyron Griffithsii* Scribn. & Smith, *A. dasystachyum* (Hook.) Scribn., *A. trachycaulum* (Link) Malte, *Stipa spartea* Trin. var. *curtiseta* Hitchc., *S. columbiana* Macoun, *Poa Cusickii* Vasey, and *Avena Hookeri* Scribn. Grasses of less common occurrence are *Agropyron spicatum* (Pursh) Scribn. & Smith, *A. Smithii* Rydb., *A. Smithii* var. *molle* (Scribn. & Smith) Jones, *Stipa Richardsoni* Link, *S. viridula* Trin., *Poa interior* Rydb., *P. Canbyi* (Scribn.) Piper, *P. juncifolia* Scribn., *Calamagrostis montanensis* Scribn., *Bromus marginatus* Nees, *Elymus condensatus* Presl., and *Muhlenbergia* spp. The chief sedge is *Carex Eleocharis* Bailey, while *C. heliophila* Mack. occurs frequently, *C. obtusata* Lilj., *C. siccata* Dewey, *C. xerantica* Bailey, and *C. scirpiformis* Mack., occasionally. Shrubs are important elements in the association. *Rosa* spp. and *Potentilla fruticosa* L. are scattered in the grassland, while *Symphoricarpos occidentalis* Hook., *Elaeagnus argentea* Pursh, *Amelanchier alnifolia* Nutt., *Prunus melanocarpa* (A. Nels.) Rydb., and *Salix Bebbiana* Sarg. are generally localized and tend to form societies within the association. In the more sheltered and mesic areas, distinct willow thickets are formed, with *Salix Bebbiana* as the dominant species (Fig. 3). The association is characterized by a large number of herbaceous forbs, some of them showing a high degree of fidelity, others tending to occur locally in considerable abundance.

Leading species include *Geranium viscosissimum* F. & M. (Fig. 5), *Pulsatilla ludoviciana* (Nutt.) Heller, *Lithospermum ruderale* Lehm., *Liatris punctata* Hook., *Lupinus leucopsis* Agardh., *Allium cernuum* Roth., *Thermopsis rhombifolia* (Nutt.) Richards., *Achillea millefolium* L., *Galium boreale* L., *Aster Geyeri* (A. Gray) Howell, *Erigeron conspicuus* Rydb., *E. caespitosus* Nutt., *Potentilla* spp., *Antennaria* spp., *Artemisia gnaphalodes* Nutt., *A. pacifica* Nutt., *Balsamorrhiza sagittata* (Pursh) Nutt. (Fig. 6), *Solidago glaberrima* Martens, *S. decumbens* Greene var. *oreophila* (Rydb.) Fernald, *S. missouriensis* Nutt., *Comandra pallida* A. DC., *Cerastium arvense* L., *Hedysarum alpinum* L. (varieties), *H. sulphurescens* Rydb., *Thalictrum venulosum* Trelease, *Oxytropis gracilis* (A. Nels.) Jones, *O. splendens* Dougl., *Vicia sparsifolia* Nutt., *Anemone cylindrica* A. Gray, *A. globosa* Nutt., *Gaillardia aristata* Pursh, *Androsace puberulenta* Rydb., *Sieversia ciliata* (Pursh) D. Don, *Agoseris glauca* (Nutt.) Greene var. *dasycephala* (T. & G.) Jepson, *Viola adunca* J. E. Smith, *Zygadenus gramineus* Rydb., *Fragaria* sp., *Lychnis Drummondii* (Hook.) S. Wats., *Delphinium bicolor* Nutt., *Cheirinia inconspicua* (S. Wats.) Rydb., and *Artemisia frigida* Willd. Species of only occasional or rare occurrence include *Ranunculus cardiophyllus* Hook., *R. affinis* R. Br., *Paronychia sessiliflora* Nutt., *Astragalus striatus* Nutt., *A. goniatus* Nutt., *A. flexuosus* Dougl., *Zizia cordata* (Walt.) Koch, *Penstemon nitidus* Dougl., *P. confertus* Dougl., *P. procerus* Dougl., *Dodecatheon Cusickii* Greene, *D. pauciflorum* (Durant) Greene, *Solidago mollis* Bartl., *Vicia americana* Muhl., *Besseya wyomingensis* (A. Nels.) Rydb., *Castilleja* spp., *Hieracium canadense* Michx., *Plantago septata* Morris, *Heuchera flabellifolia* Rydb. var. *typica* R.B.L., *Senecio canus* Hook., *S. hydrophilus* Nutt., *Erigeron glabellus* Nutt. var. *pubescens* Hook., *Gentiana plebeja* Cham., *G. affinis* Griseb., *Bupleurum americanum* Coult. & Rose, *Lomatium simplex* (Nutt.) Macbr. var. *leptophyllum* (Hook.) Mathias, *Astragalus bisulcatus* A. Gray, and *Polytrichum piliferum* Schreb.

This association is closely allied to the "mixed prairie" as understood by leading American ecologists (7, 16) and especially to the submontane type of mixed prairie in the Great Plains (6). It is similar also to the so-called "northern prairie" as described by the present writer (9) for the parkland region of central Alberta, differing however, in having as leading species, *Festuca idahoensis, Danthonia* spp., *Stipa spartea* v. *curtiseta, Stipa columbiana, Poa Cusickii, Carex Eleocharis, Geranium viscosissimum, Balsamorrhiza sagittata,* and *Lupinus leucopsis,* while lacking an abundance of *Agropyron trachycaulum, Stipa viridula, Carex obtusata, Cerastium arvense, Sieversia ciliata, Vicia americana, Thalictrum venulosum, Zizia cordata,* and certain other species. Further investigation is needed to establish the inter-relationships of the submontane prairie of the United States, the *Festuca–Danthonia* association of southwestern Alberta and the parkland prairie of central Alberta, as well as the relations of these associations to other contiguous types. The *Festuca–Danthonia* association also shows affiliations with the so-called Palouse prairie of eastern Oregon and Washington, southern Idaho, and northern Utah, and elements of which extend eastward through the Rocky

PLATE I

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FIG. 2. *Festuca–Danthonia prairie and aspen groves in the black soil zone north of Waterton Lakes Park. A few small conifers on the steep slope at the left.* FIG. 3. *Parkland in the black soil belt north of Waterton Lakes Park. Willow societies on the low ground.*

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FIG. 4. *Bouteloua–Stipa association, showing Bouteloua gracilis, Stipa spp., Artemisia frigida, and other species.* FIG. 5. *Geranium viscosissimum in the Festuca–Danthonia prairie, south of Pincher Creek.* FIG. 6. *The Festuca–Danthonia association west of Pincher Creek, showing Balsamorrhiza sagittata (large plant), Zygadenus gramineus, and other forbs.*

Mountains into Wyoming and Montana (6, 12). It is now evident that important elements of the Palouse prairie extend into Alberta, notably, *Festuca idahoensis*, *Stipa columbiana*, *Agropyron spicatum*, *Geranium viscosissimum*, *Lithospermum ruderale*, and *Balsamorrhiza sagittata*.

Agropyron–Stipa–Carex Associes

This associes occupies large areas of the region, especially in the shallow black soil zone. Here certain secondary species of the adjoining associations are abundant, notably *Agropyron Smithii*, *A. dasystachyum*, *A. Griffithsii*, *Stipa spartea* v. *curtiseta*, *S. viridula*, and *Carex Eleocharis* (Table I). On heavier lowland soils, the *Agropyron* species, especially *A. Smithii*, predominate while on lighter and better drained soils, the *Stipa* species are abundant. The associated plants are those of the contiguous *Bouteloua–Stipa* and *Festuca–Danthonia* associations. These species are found in a great variety of mixtures in the different facies of the associes.

A number of factors appear to have operated in the production of this associes. In general, *Agropyron* and *Stipa* species seem to be favoured by the particular climatic and edaphic conditions prevailing in the shallow black soil zone. Yet there is considerable evidence that an associes formed by these grasses is subclimax and that the climax for the zone is the *Festuca–Danthonia* association. This association was probably only partially realized when man came upon the scene. Through man's activities, the grassland has reverted to an earlier phase that might properly be termed disclimax (5) rather than subclimax. The disturbance caused by grazing, especially overgrazing, seems to have been largely responsible for the reduction of the highly palatable fescues and their replacement by *Agropyron*, *Stipa*, *Carex Eleocharis*, and certain forbs, e.g. *Artemisia frigida*. There is evidence also that soil drifting from adjoining cultivated fields has caused killing of many of the virgin species and that *Agropyron Smithii* has then dominated the grassland areas thus covered with wind-blown soil.

Poisonous Species of the Prairie

A number of the prairie species are poisonous to livestock. The more important of these are the low larkspur (*Delphinium bicolor*), the lupines (*Lupinus* spp.), death camas (*Zygadenus gramineus*), loco weeds (*Oxytropis* spp.), and the two-grooved vetch (*Astragalus bisulcatus*). The latter species is known to be toxic because of its selenium content. In the United States, it has been shown that this vetch and several other species take up large quantities of selenium from certain soils. Seleniferous plants are responsible for two somewhat different types of poisoning in livestock, namely, alkali disease and blind staggers. A few of these seleniferous species occur in Alberta but little is known about their selenium content or toxicity. Seleniferous species collected in connection with the present investigation are *Astragalus bisulcatus*, *A. pectinatus*, *Atriplex Nuttallii* S. Wats., and *Nuttallia decapetala* (Pursh) Greene. The narrow-leaved vetch, *A. pectinatus*, is rather common in parts of southern Alberta and should be carefully investigated in

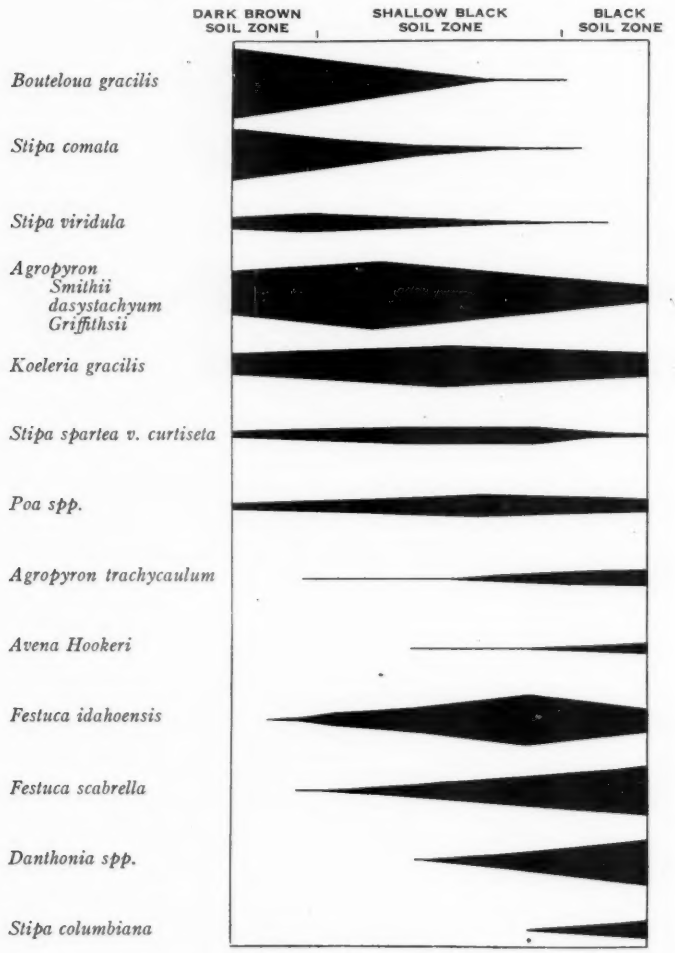

FIG. 7. *Graphical representation of the leading prairie grasses in southwestern Alberta, showing the relative abundance of species and species groups from east to west across the soil zones.*

regard to its selenium content in different areas, the selenium content of different parts of the plant, and the selenium in the supporting soils. In this connection, an observation made a few years ago by the former Provincial apiarist, S. Hillerud, is of interest. In attempting to account for the high mortality of foraging bees, Hillerud found convincing evidence of the bees having been poisoned after going to flowers of *Astragalus pectinatus*. As stated by Walker *et al.* (14): "The whole matter of possible selenium poisoning in Alberta can be cleared up only by an intensive survey of the area from the standpoint of selenium content of the soil and all types of vegetation".

Poplar Vegetation

Many of the sheltered positions provided by the rough topography near the mountains are characterized by poplar vegetation. North and east-facing slopes of valleys, slough depressions, ridges, and knolls may bear aspen groves (Figs. 2, 3, and 8). The flats of streams and rivers are commonly occupied by certain other species of poplar.

Poplar Vegetation of River Flats

In the black soil zone, the flats and margins of rivers and streams are characterized by balsam or black poplars, especially *Populus trichocarpa* T. & G. and the variety *hastata* (Dode) Henry. *Populus tacamahacca* Mill. also occurs in places, and there is evidence of hybrids between these balsam poplars. The poplars are sometimes accompanied by *Betula microphylla* Bunge and *Alnus tenuifolia* Nutt., and commonly by willows, including *Salix lutea* Nutt., *S. caudata* (Nutt.) Heller, *S. exigua* Nutt., *S. melanopsis* Nutt., and *S. monochroma* Ball. The stony and gravelly margins of streams are further characterized by the following conspicuous herbs,—*Epilobium latifolium* L., *Physaria didymocarpa* (Hook.) A. Gray, *Astragalus pauciflorus* Hook., *Oxytropis splendens* Dougl., and *Apocynum* sp. Species of muddy or grassy river banks include *Juncus nodosus* L., *J. longistylis* Torr., *J. Dudleyi* Wieg., *J. Tracyi* Rydb., *J. saximontanus* A. Nels., *J. balticus* var. *montanus* Engelm., *J. alpinus* var. *rariflorus* Hartm., *Eleocharis uniglumis* (Link) Schultes, *E. calva* Torr., *Carex microptera* Mack., *C. lanuginosa* Michx., and *C. festivella* Mack.

In available manuals and bulletins there is considerable confusion with respect to *Populus trichocarpa* and the variety *hastata*. Rydberg regards the latter as a distinct species. Sudworth (13) does not admit typical *P. trichocarpa* to the Rocky Mountain region, considering it to be mainly confined to California. Actually, both *P. trichocarpa* and the variety *hastata* are common in the vicinity of Waterton and northward to the Oldman River. Moreover, these two forms seem to intergrade, evidence of hybridization.

Eastward in the region, *P. trichocarpa* and variety *hastata* are largely replaced by *P. angustifolia* James, the lanceleaf cottonwood. *P. tacamahacca* also occurs, apparently only locally, while *P. acuminata* Rydb. and *P. Sargentii* Dode are found sporadically in the eastern part of the region surveyed. In the river valley at Lethbridge, the latter species are accompanied by trees showing evidence of hybridity. Associated with these various cottonwoods are a number of willows, notably *Salix lutea* Nutt., *S. caudata* (Nutt.) Heller, *S. interior* var. *pedicellata* (And.) Ball, *S. melanopsis* Nutt., and *S. amygdaloides* And.

Aspen Poplar Consociation

Throughout the greater part of the region near the mountains, aspen vegetation occurs mainly in the form of small isolated groves, occupying positions that afford protection against insolation and prevailing winds.

These groves are chiefly confined to depressions and northeast slopes, and together with the associated prairie form a "parkland" (Figs. 2, 3, and 8). In the southeastern part of Waterton Lakes Park, and in the immediately adjoining areas, the aspen consociation is quite extensive. Rarely is the aspen, *Populus tremuloides*, accompanied by *P. tacamahacca*. Nor is the aspen ordinarily accompanied by other tree species, except on foothill and mountain slopes where it gives way to conifers, especially lodge-pole pine, Douglas fir, and white spruce.

The aspen stands are, in the main, even-aged and rather young, obviously owing to burning of the areas in comparatively recent years. The ages of the stands investigated ranged from about 20 to 40 years. The stands are generally of low stature, growth in height having been retarded by the prevailing dry winds. Groves in the more exposed positions have truncated tops and the characteristic wind-blown habit.

Beyond a certain height, growth is extremely slow, as was shown by a particular stand in which a small group of centrally placed trees were older than the others. The older trees, approximately 38 years in age, had evidently survived a fire of about 22 years before, the younger trees being mainly 20 years old. The older trees had a *D.B.H.* of 7 to 9 in., the younger trees 4 to 5 in. Yet the older trees were no taller than the younger ones, both ranging from 25 to 28 ft. Incidentally, the use of dominant tree height as a measure of site would place this grove in a very low site-index category (9). Obviously, the site of the grove is a poor one for growth of trees beyond a very limited height and probably also for growth beyond a certain diameter. This is due, however, not to poor soil or topography but rather to the prevailing winds. Worthy of note in this connection is a statement by Parker (10) that average diameter of trees correlated with height and age provides a better measure of site than merely height and age. Parker's conclusion is supported by the foregoing observation.

The aspen consociation tends to invade adjoining prairie by the production of root sprouts. This tendency is doubtless counteracted to some extent by prairie fires and by grazing, to a considerable extent by insolation but, in the main by the prevailing strong, desiccating winds. In the parkland of central Alberta, extension of aspen into adjoining prairie was considered to be largely prevented by fires (9). Clements *et al.* (6) minimize the influence of burning in this connection. They maintain that "migration by climatic compulsion has carried trees and shrubs into the grassland and the laggards at the next turn of the cycle have supplied the relicts upon which man has operated through fire, grazing and cultivation". Obviously, in a discussion of this kind, distinction must be made between the larger climatic shifts of the past and those currently operative. It may have been, as Clements *et al.* suggest, that the aspen parkland of Western Canada originated "as the boreal forest straggled northward after a climatic shift to the warm-dry phase", the aspen vegetation remaining as groves in the more moist and sheltered positions while prairie invaded the drier areas. As already stated (9) the aspen groves

PLATE III

8

9

FIG. 8. *Rough parkland west of Pincher Creek. Grassland on the drier slopes, poplar and other wooded vegetation on the more sheltered slopes. Willow and other societies in the valley. On the rocky exposures (upper left) small Pinus flexilis occurs.* FIG. 9. *Foothills a short distance west of the area shown in Fig. 8. A small patch of prairie vegetation in the foreground. Poplar, willow, and coniferous vegetation elsewhere.*

in the parkland of central Alberta are tending to encroach upon the prairie, and, in the absence of burning, succession is generally taking place in this direction. Admittedly, grazing, cultivation, and other factors are also operative in either retarding or favouring the extension of the aspen into the prairie. In central Alberta, therefore, current climatic conditions favour the invasion of the prairie by aspen. On the other hand, in the parkland of southwestern Alberta, the present climate seems to be less favourable to the enlargement of the aspen groves.

Several interrelated factors doubtless operate in restricting the aspen to the more sheltered positions. Insolation, high soil temperatures, high air temperatures, high evaporation rate, and strong, westerly winds characterize the south and southwest slopes that are occupied by prairie vegetation and from which the aspen is excluded. Of these factors, winds are of paramount importance, both in the growing and in the resting periods of the year. As already mentioned, the Chinook winds probably cause killing of plants during the winter and early spring.

A small number of aspen stands located in the foothills west of Pincher Creek and in the vicinity of Waterton were investigated as to ecological structure and floristic composition. These samples are considered to be representative of the aspen vegetation of the region and to justify the following characterization.

The aspen consociation consists of as many as five rather well-defined layers or strata, viz. (*a*) taller trees, almost all aspens, forming a practically continuous canopy; (*b*) smaller trees and larger shrubs, usually a sparse or only locally prominent layer; (*c*) lower shrub layer, commonly well developed, but somewhat obscured in late summer by members of the next layer; (*d*) taller herbs, often an almost continuous stratum; (*e*) lower herbs, relatively a poorly developed layer.

As already stated, *Populus tremuloides* Michx. is only locally accompanied by other tree species, these being *Populus tacamahacca* Mill. on rather low places, *Betula microphylla* Bunge, *Pseudotsuga Douglasii* Carr., *Pinus contorta* Loud. var. *latifolia* Engelm., and *Picea glauca* Voss in the foothills and on mountain slopes. The more important smaller trees and larger shrubs are *Salix Bebbiana* Sarg. and *Amelanchier alnifolia* Nutt. Those of localized or infrequent occurrence include *Cornus stolonifera* Michx., *Prunus melanocarpa* (A. Nels.) Rydb., *P. pennsylvanica* L., *Salix discolor* Muhl., and *Crataegus Douglasii* Richards. The lower shrub layer is characterized by *Rosa acicularis* Lindl., *R. Woodsii* Lindl., and *Symphoricarpos albus* (L.) Blake, while species of lesser importance include *Rubus parviflorus* Nutt., *R. idaeus* L., *Spiraea lucida* Dougl., *Ribes oxyacanthoides* (L.) Mill., *Lonicera glaucescens* Rydb., and *Clematis columbiana* (Nutt.) T. & G. The taller herb stratum includes the following leading species,—*Agropyron trachycaulum* (Link) Malte, *Aster Lindleyanus* T. & G., *Galium boreale* L., *Epilobium angustifolium* L., *Vicia americana* Muhl., *Lathyrus ochroleucus* Hook., and *Thalictrum* spp., and the following of less frequent occurrence,—*Calamagrostis* spp., *Bromus* spp.,

Poa palustris L., *Carex* spp., *Aster conspicuus* Lindl., *Aster* spp., *Angelica Lyallii* S. Wats., *Leptotaenia multifida* Nutt., *Osmorrhiza* spp., *Sanicula marilandica* L., *Geranium Richardsonii* Fisch. & Trautv., *Actaea rubra* (Ait.) Willd., *Geum* spp., *Monarda menthaefolia* Benth., and *Disporum* spp. Included in the lower herb stratum are the following,—*Viola canadensis* L., *Fragaria* spp., *Pyrola asarifolia* Michx., *Smilacina stellata* Desf., and *Berberis repens* Lindl. The total number of vascular species found in the aspen consociation was ninety-six. This number would doubtless be considerably increased by more extensive investigation.

This aspen consociation may be compared with that of central Alberta for which 122 vascular species have been recorded (9). The two communities are doubtless sufficiently alike in physiognomy, internal structure, and floristic composition to be classified as variants of the same aspen consociation. At the same time, there are interesting differences, especially in floristic composition. The aspen consociation of southwestern Alberta is apparently lacking in *Corylus rostrata* Ait., *Viburnum pauciflorum* Pylaie, *Aralia nudicaulis* L., *Cornus canadensis* L., *Maianthemum canadense* Desf. and in certain sedges, mosses, and other important plants of the more northern consociation, while it includes a number of species not reported for the north, e.g., *Rubus parviflorus*, *Spiraea lucida*, *Leptotaenia multifida*, *Angelica Lyallii*, *Glycosma occidentalis* Nutt., *Thalictrum megacarpum* Torr., and *Berberis repens*. A critical analysis of the aspen vegetation in Alberta must await more extensive field work.

Coniferous Vegetation

Two coniferous types of vegetation, namely, limber pine and Douglas fir communities, are found on the rocky, ridge-like outliers of the mountains in the black soil zone, a region occupied mainly by *Festuca–Danthonia* prairie and aspen poplar vegetation. These coniferous types are described more fully below. Some of the rocky exposures and likewise a few of the larger foothills support a growth of junipers, namely, *Juniperus horizontalis* Moench and *J. sibirica* Burgsd. White spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta* var. *latifolia*) are associated with Douglas fir, limber pine, and the poplars on many of the larger foothills (Fig. 9). Individually, these species form practically pure stands in localized areas. Prairie vegetation also occurs on certain slopes of the larger foothills and even of some of the outer mountains where it seems to merge with the vegetation of talus slopes and rocky ledges. Thus, a number of coniferous and other types of vegetation are variously intermixed in a comparatively small area possessing a diversity of edaphic features. These vegetational types present many intriguing ecological and floristic problems.

Limber Pine Vegetation

This is the characteristic vegetation of the so-called "pine ridges", especially the tops and drier slopes of these ridges. The most conspicuous species, limber pine (*Pinus flexilis*), commonly shows a dwarfed and distorted habit

with extensive killing of branches on the windward side of the crown (Figs. 8 and 10). While limber pine might be described as the dominant species, it actually forms an open community containing many exposed areas of various sizes. Only locally do the pines provide shade and otherwise influence accompanying species. In most parts of the ridges, the rock has weathered to form a thin, loose, shaly soil, while in localized areas the rocky exposures are practically unweathered. The flora of these ridges, especially in the region west of Pincher Creek, was given rather close study. The species are listed below under appropriate headings and in approximate order of their frequency in each kind of situation. Certain species are found in more than one of the three situations, while other species are definitely restricted in their occurrence.

Species on bare rock exposures and unshaded: *Pinus flexilis* James, *Arctostaphylos uva-ursi* (L.) Spreng., *Juniperus horizontalis* Moench, *Phlox alyssifolia* Greene, *Physaria didymocarpa* (Hook.) A. Gray, *Sedum stenopetalum* Pursh, *Astragalus pauciflorus* Hook,, *Juniperus sibirica* Burgsd., *Eriogonum flavum* Nutt., *Musineon* sp.

Species on shallow soil in the partial shade of limber pine: *Galium boreale* L., *Aster conspicuus* Lindl., *Rosa* spp., *Pseudotsuga Douglasii* Carr., *Agropyron spicatum* (Pursh) Scribn. & Smith, *Shepherdia canadensis* (L.) Nutt., *Penstemon confertus* Dougl., *Heuchera* sp., *Hieracium griseum* Rydb., *Arabis divaricarpa* A. Nels., *Draba incerta* Payson, *D. oligosperma* Hook., *Cerastium arvense* L., *Townsendia Parryi* D. C. Eaton, *Phacelia sericea* (Graham) Gray, *Glycosma occidentalis* Nutt., *Disporum trachycarpum* S. Wats., *Goodyera decipiens* Hubbard, *Carex Hoodii* Boott., *Leptotaenia multifida* Nutt., *Delphinium bicolor* Nutt., *Besseya wyomingensis* (A. Nels.) Rydb., *Polemonium pulcherrimum* Hook. var. *parviflorum* (Nutt.) A. Nels.,*Androsace puberulenta* Rydb., *Populus tremuloides* Michx., *Lonicera glaucescens* Rydb., *Clematis columbiana* (Nutt.) T. & G., *Arabis Holboellii* Hornem., *A. Nuttallii* Robinson, *Saxifraga rhomboidea* Greene, *Dodecatheon Cusickii* Greene.

Species on shallow soil and unshaded: *Arctostaphylos uva-ursi* (L.) Spreng., *Juniperus horizontalis* Moench, *Selaginella densa* Rydb., *Agropyron spicatum* (Pursh) Scribn. & Smith, *Festuca idahoensis* Elmer, *Koeleria gracilis* Pers., *Agropyron dasystachyum* (Hook.) Scribn., *Poa* spp., *Potentilla fruticosa* L., *Rosa* spp., *Artemisia frigida* Willd., *A. pacifica* Nutt., *Cryptantha Bradburiana* Payson, *Erigeron caespitosus* Nutt., *E. compositus* Pursh, *Antennaria reflexa* E. Nels., *A. aprica* Greene, *Galium boreale* L., *Aster conspicuus* Lindl., *Cerastium arvense* L., *Thermopsis rhombifolia* (Nutt.) Richards., *Allium cernuum* Roth, *Chrysopsis villosa* (Pursh) Nutt., *Astragalus pauciflorus* Hook., *Penstemon nitidus* Dougl., *P. eriantherus* Pursh, *Penstemon confertus* Dougl., *Campanula rotundifolia* L., *Solidago glaberrima* Martens, *S. decumbens* Greene var. *oreophila* (Rydb.) Fern., *Achillea millefolium* L., *Paronychia sessiliflora* Nutt., *Phlox Hoodii* Richards., *Anemone globosa* Nutt., *Castilleja fasciculata* A. Nels., *Heuchera* sp., *Juniperus sibirica* Burgsd., *Shepherdia canadensis* (L.) Nutt., *Lychnis Drummondii* (Hook.) S. Wats., *Danthonia intermedia* Vasey, *Avena*

Hookeri Scribn., *Calamagrostis purpurascens* R. Br., *Lupinus leucopsis* Agardh., *Linum Lewisii* Pursh, *Eriogonum flavum* Nutt., *Hedysarum sulphurescens* Rydb., *Cogswellia macrocarpa* (Nutt.) Jones, *Musineon divaricarpum* (Pursh) Raf. var. *Hookeri* (Nutt.) Mathias, *Polemonium pulcherrimum* Hook., *Besseya wyomingensis* (A. Nels.) Rydb., *Phacelia sericea* (Graham) Gray, *P. leucophylla* Torr., *P. linearis* (Pursh) Holz., *Carex filifolia* Nutt., *Stipa spartea* Trin. var. *curtiseta* Hitchc., *Calamovilfa longifolia* (Hook.) Scribn., *Zygadenus elegans* Pursh, *Senecio canus* Hook., *Hieracium griseum* Rydb., *Arenaria propinqua* Richards., *Collinsia parviflora* Dougl., *Astragalus missouriensis* Nutt., *Geoprumnon succulentum* (Richards.) Rydb., *Linum compactum* A. Nels., *Arabis Holboellii* Hornem., *Draba oligosperma* Hook., *Apocynum cannabinum* L., *Townsendia Parryi* D. C. Eaton, *Juncus confusus* Coville, *Populus tremuloides* Michx., *Physaria didymocarpa* (Hook.) A. Gray, *Cheirinia inconspicua* (S. Wats.) Rydb., *Aster campestris* Nutt., *A. adscendens* Lindl., *Androsace puberulenta* Rydb., *Arabis Nuttallii* Robinson, *Epilobium adenocladon* (Haussk.) Rydb., *Polygonum Engelmannii* Greene, *Danthonia unispicata* Munro.

Douglas Fir Vegetation

Douglas fir occurs in a number of situations including sandy and gravelly foothill slopes, and the more protected slopes of rocky pine ridges. The latter were examined in an area 6 to 10 miles west of Pincher Creek. Here there are dense stands of rather young fir on some of the sheltered east and northeast steep slopes of ridges. Apparently Douglas fir is unable to endure the effects of the strong, desiccating westerly winds. The lower, gentler slopes below the fir stands are occupied by aspen and various shrubs, these in turn merging with the prairie (Fig. 11). In places, the fir forms a close stand, with a sparse ground vegetation. Elsewhere, the fir stand is more open and the accompanying vegetation composed of species commonly found with aspen, limber pine, or prairie grasses, as well as a number not encountered in these associations.

The following species, arranged in approximate order of their abundance and frequency were recorded for the Douglas fir vegetation of pine ridges: *Pseudotsuga Douglasii* Carr., *Rosa* spp., *Agropyron trachycaulum* (Link) Malte, *Rubus parviflorus* Nutt., *Symphoricarpos* sp., *Amelanchier alnifolia* Nutt., *Acer Douglasii* Hook., *Pinus flexilis* James, *Calamagrostis canadensis* (Michx.) Beauv., *Aster conspicuus* Lindl., *Clematis columbiana* (Nutt.) T. & G., *Poa palustris* L., *Heracleum lanatum* Michx., *Glycosma occidentalis* Nutt., *Smilacina racemosa* (L.) Desf., *Actaea rubra* (Ait.) Willd., *Disporum trachycaulum* S. Wats., *Hieracium griseum* Rydb., *Leptotaenia multifida* Nutt., *Solidago glaberrima* Martens, *Erigeron speciosus* (Lindl.) DC., *Ribes oxyacanthoides* (L.) Mill., *Silene Menziesii* Hook., *Lychnis Drummondii* (Hook.) S. Wats., *Hackelia floribunda* Lehm., *Agropyron spicatum* (Pursh) Scribn. & Smith, *Heuchera cylindrica* var. *septentrionalis* R.B.L., *Populus tacamahacca* Mill., *Spiraea lucida* Dougl., *Lonicera glaucescens* Rydb., *Rumex* sp., *Phacelia sericea* (Graham) Gray, *Androsace puberulenta* Rydb., *Delphinium bicolor*

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FIG. 10. *Rocky pine ridge, about six miles west of Pincher Creek, showing Pinus flexilis on the southwest slope. Prairie vegetation on the better soil at the right.* FIG. 11. *Northeast slope of the ridge shown in Fig. 10, with Douglas fir in the more protected situations. Elsewhere aspen, various shrubs, and grasses dominate.*

Nutt., *Penstemon Lyallii* A. Gray, *Calochortus apiculatus* Baker, *Erythronium grandiflorum* Pursh, *Drymocallis pseudorupestris* (Pursh) Rydb., *Phacelia linearis* (Pursh) Holz., *Dodecatheon Cusickii* Greene, *Arabis Nuttallii* Robinson, *Cystopteris fragilis* (L.) Bernh., *Woodsia* sp., *Claytonia lanceolata* Pursh, *Anaphalis margaritacea* (L.) B. & H., *Pyrola asarifolia* Michx., *Berberis repens* Lindl., *Calamagrostis purpurescens* R. Br., *Agoseris glauca* var. *dasycephala* (T. & G.) Jepson, *Castilleja rhexifolia* Rydb., *Arnica cordifolia* L., *Senecio* sp., *Urtica* sp., *Hedysarum sulphurescens* Rydb., *Geranium Richardsonii* Fisch. & Trautv.

Discussion

An attempt has been made to consider the vegetation of the region in relation to climatic and edaphic factors. As already emphasized, the proposed classification of grassland is to be regarded as a temporary expedient, a scheme to be tested by further studies in the same area and in adjoining prairie regions. Some attention has been given to current trends and fluctuations of the vegetational communities. To determine precisely the natural course of events, and how this course is being altered by human influence, would require critical study over a long period of time. Investigation of grasslands in the United States (15) has revealed marked fluctuations in the vegetation induced by the extreme climatic changes, especially excessive drought, of the past decade. The importance of factors operating at comparatively long intervals becomes increasingly apparent.

Much to be desired is a knowledge of the major climatic and geological changes since the last glaciation, especially those changes influencing the establishment of grasses and aspen in the region. Conversely, a better understanding of current trends in the natural vegetation, and of climate–vegetation–soil relationships would doubtless throw some light on climatic fluctuations and geological changes of postglacial time.

Data gathered in this investigation may be useful in the solution of certain floristic problems. Mention has been made of Palouse elements in the grassland of the region. These and certain other western species may have entered the region from the south, or they may have migrated through the mountains farther north, for example, through the Crow's-Nest Pass. The indications are that such prairie species as *Agropyron spicatum*, *Stipa columbiana*, *Festuca idahoensis*, *Geranium viscosissimum*, and *Balsamorrhiza sagittata* reached the area by either one, or by both, of these routes. The distribution of Douglas fir east of the Continental Divide indicates that this species came into Alberta from the west through passes in the mountains and not from the south along the Divide. Probably *Populus trichocarpa* moved eastward along the same courses. Other western species, e.g. *Xerophyllum tenax* (Pursh) Nutt., may have migrated along higher mountain routes into southwestern Alberta. *Pinus monticola* Dougl. on an eastern mountain slope at Waterton (drawn to the writer's attention by W. C. McCalla) and *Philadelphus Lewisii* Pursh, in the same location, are interesting and unexplained extensions of western species into Alberta. The vagaries of species distribution may be further

illustrated by reference to Devil's Club, *Oplopanax horridum* (J. E. Sm.) Miq., which is common on the western slopes of the Rocky Mountains and which occurs only rarely and sporadically over a considerable range from Glacier National Park and Waterton Lakes Park to Lesser Slave Lake, east of the Divide, and again far eastward at Isle Royal, Lake Superior. The solution of these and other floristic problems presented by the region investigated would seem to require additional distributional records of species and also a clearer understanding of climatic and geological changes associated with the Cordilleran and Keewatin glaciations and during the postglacial period.

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